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*Chironomus aculeata*, and *Nephtys* spp.) were collected. Similar mass migration of species to the sediment surface has been recorded during trawling in the North Sea, off the northeast coast of New Zealand, and on the middle Atlantic continental shelf off New Jersey. Many of the species involved in the trawls were deep dwelling and rarely taken in grab samples under normal dissolved oxygen conditions.

The spionid polychaete, *Malacoceros fuliginosus*, was observed in experiments to change its behavior in declining oxygen concentrations. Under fully aerobic conditions this species lives below the sediment surface in burrows. When oxygen concentrations drop below 2.4 cm<sup>3</sup> O<sub>2</sub>/liter the animals emerge from their burrows and rise partly up in the water column. When oxygen concentrations fall below 0.5 cm<sup>3</sup> O<sup>3</sup>/liter, the *M. fuliginosus* begin undulatory body movements and ultimately form rapidly weaving clumps of animals. This behavior likely causes water from higher up in the microgradient layer (presumably with higher oxygen content) to come in contact with the worms.

**Metabolic switching.** With the intensification or persistence of hypoxia there is a metabolic switching in favor of near anaerobic or anaerobic pathways. During anoxia most polychaetes have some ability for facultative anaerobiosis. As anaerobic conditions approach the sediment surface, sulfur and anaerobic microbes experience population explosions. Thus, the quality of the habitat for polychaetes is further reduced. With continued hypoxia, anoxic conditions and hydrogen sulfide eventually reach the sediment surface and extend into the water column, and mass mortality results.

**Population dynamics.** When bottom waters are reoxygenated, recolonization processes begin to restore polychaete populations. Larval tolerance of hypoxia is critical to the early recolonization of hypoxia-stressed habitats, particularly in organically enriched habitats which are prone to develop hypoxia and anoxia due to high chemical and biological oxygen demand. There is great advantage to being the first species to reenter a defaunated habitat, and polychaetes generally are the first. Larvae of spionid polychaete *S. benedicti*, for example, were found to be unaffected when exposed to short-term hypoxia (92 h; 14% saturation). This tolerance of hypoxia gives *S. benedicti* the opportunity to be the first to utilize food resources left behind during hypoxic and anoxic events.

The ecological consequences of periodic hypoxia on benthic organisms are varied, but it is clear that hypoxia functions as a mechanism for regulating benthic population dynamics. In affected areas, temporal and spatial patterns in benthic organism abundance and species composition are related to the occurrence of hypoxia. Because of their broad physiological tolerance of hypoxia polychaete species tend to dominate hypoxia-stressed estuarine and marine communities around the world. Two particularly tolerant species are the terebellid

*Loimia medusa* and the spionid *Paraprionospio pinnata*. Other polychaetes (the spionid *S. benedicti* and the capitellid *Mediomastus ambiseta*) that are known to thrive in organic enrichment areas are more sensitive to hypoxia and are often eliminated during severe hypoxia and anoxia; however, these same species are the first to recolonize an area with the return of normal oxygen conditions. The timing of hypoxia relative to recruitment is also critical to survivorship of newly settled individuals. For example, the summer recruitment peaks for *Podarkeopsis levifuscina* and *Pseudeurythoe paucibranchiata* both declined with the onset of hypoxia.

**Implications.** At what point permanent damage will result is difficult to assess; to date there is no large system that has recovered after development of persistent hypoxia or anoxia. Exceptions may be small systems where point effluents have ceased and recovery can be initiated from surrounding nonaffected areas. The expanding occurrence of hypoxia and anoxia continues to bring about significant structural changes in benthic communities and to affect the cycling of energy within and between ecosystems. No other environmental parameter of such ecological importance to coastal marine ecosystems has changed so drastically in such a short period as dissolved oxygen. Areas experiencing hypoxia are spreading into shallower waters with increasing frequency, and have the potential to deleteriously affect benthic organisms and complete ecosystems.

For background material SEE ANNELIDA, FRESH-WATER ECOSYSTEM; HYPOXIA; POLYCHAETA in the McGraw-Hill Encyclopedia of Science & Technology.

Robert J. Diaz; Rutgers Rosenberg

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## Precipitation (meteorology)

Precipitation sustains nearly all terrestrial plants and animals; both rain-fed and irrigated agriculture depend on an appropriate amount and distribution of annual rain and snowfall. Precipitation also initiates important hydrological processes, such as infiltration, recharge, runoff, and erosion. Although these processes support natural plant communities and make agriculture possible, they may facilitate development of serious environmental problems, such as the contamination of surface waters with excess sediment, nutrients, and natural and manufactured chemicals and the adulteration of ground water via soil transport of surface-applied compounds. Understanding how precipitation may vary in the landscape permits identification of areas of

high impact, better focusing of management efforts, maximization of agricultural productivity, and minimization of potentially adverse environmental hazards.

**Wind-terrain interactions.** Interactions of wind with Earth surface relief influence rainfall distribution in the landscape.

Wind-terrain interactions that alter rainfall uniformity across the landscape can occur at several spatial scales. Large-scale effects on rainfall distribution can occur over distances of 400 km (250 mi). Here, winds influence the trajectory of moisture-laden air masses as they travel across hill or mountain ranges with relief of 300+ m (1000+ ft). A similar interaction occurs for small-scale landforms, where the extent of horizontal influence is less than 80 km (50 mi) and relief is less than 100 m (330 ft). Furthermore, microscale impacts can occur even over horizontal distances less than 30 m (100 ft), such as a farmer's field. In this case, winds traverse low hills less than 10 m (30 ft) high and influence only the trajectory of raindrops.

Wind-terrain interactions influence both cyclonic and convective precipitation. Cyclonic storms produce precipitation when warm moist air is forced aloft by horizontal collision of airstreams in an area of low pressure, for example, the depression (low pressure) associated with a cold-front wave. These depressions are extensive, commonly encompassing an area in excess of 100,000 km<sup>2</sup> (38,600 mi<sup>2</sup>). They produce generally continuous precipitation of low to moderate intensity, and raindrops are of relatively small or medium size. Convective storms are created when moist air that is warmed at the Earth's surface rises, or is forced to rise, into a cooler unstable atmosphere. The rising air mass cools, forming clouds and precipitation. Because the upper atmosphere is unstable, the parcel will continue to rise and produce further rainfall. Resulting thunderstorms usually produce high-intensity rainfall and more large-sized raindrops but are limited in duration ( $\frac{1}{2}$ –1 h per storm) and extent (20–50 km<sup>2</sup> or 7–20 mi<sup>2</sup>).

**Large-scale impacts.** When a moist airflow intercepts a mountain front, it is deflected upward. This deflection may increase precipitation (1) by causing horizontal convergence and uplift as the airstream is channeled upward through mountain valleys or forced over steep windward slopes and (2) by promoting convective storm development by imparting an initial upward movement to surface air.

**Upslope and cyclonic rain.** In the first case, upslope rain is produced when a warm moist air mass is lifted into a stable atmosphere. Forced uplift brings the air mass to the saturation point and induces further condensation and raindrop formation. Upslope rain will also occur in conjunction with passing cyclonic storms. The effect that the topographic component has on precipitation becomes greater as the air mass is lifted to higher elevations, as is evidenced on the U.S. Pacific Coast mountain ranges at middle and higher latitudes. At lower latitudes,

the topographic component reaches its maximum effect at middle elevations and decreases at higher altitudes because tropical moisture is concentrated near the surface. Cyclonic precipitation decreases significantly to the leeward of these topographic barriers owing to drying associated with descending air. This rain shadow produces a rainfall minimum on leeward mountain slopes and adjacent valley floors.

Lifting of airflow by its interception with a mountain front increases the frequency, duration, and intensity of precipitation events associated with cyclonic storm systems. Magnitude of forced uplift and precipitation values depends on (1) the character of each site (elevation, slope, aspect), (2) the local landscape milieu, such as upwind or downwind relief, and (3) the regional landform configuration, for example, distant valley or mountain features that, by virtue of their orientation, influence large-scale air movement across the site. Annual precipitation originating from cyclonic systems becomes greater as site location changes from leeward to more windward aspects, gentle inclines to steeper hill and mountain slopes, lower to higher elevations, and positions that feature gently rising leeward relief adjacent to steeply rising leeward relief.

**Convective rain.** Convective storms triggered by large-scale wind-terrain interactions tend to develop above the mountain summit and drift downwind. Hence, maximum precipitation occurs on leeward slopes and relatively lower amounts on windward aspects. The effect of mountainous terrain on convective precipitation is less pronounced in rugged, mountainous landscapes. Complex relief is thought to reduce the efficiency with which developing storms assimilate latent energy from the atmosphere. The so-called drawing power of such storms is inhibited because the air mass lacks continuity. Thus, convective storm activity in complex physiography consists of numerous, small rain cells that produce less intense rainfall. By comparison, storms that develop over hills surrounded by a smooth plain are able to access a larger pool of energy. Rain cells can grow larger and can produce more intense precipitation of longer duration and better-defined rainfall patterns.

**Small-scale effects.** Upslope rainfall is not produced when winds propel moist air over small hills. Air masses traverse the small landform too rapidly for raindrops to form. However, forced uplift over the summit does produce local low-level condensation and clouds. Raindrops produced by passing cyclonic or convective systems fall through the low summit clouds, intercept the cloud droplets, and grow larger. The resulting rainfall distribution has a maximum that is centered over the hill summit.

Researchers have observed strong topographic effects on convective precipitation even when relief is low or moderate. For example, two zones of maximum summer rainfall observed in the Min-

opolis-St. Paul region may be caused by the upward deflection of surface winds over a low, steeply sloping physiographic barrier. Winds from the E-SSE quadrant, which predominate during summer precipitation events, become channeled along similarly oriented 18-km (11-mi) segments of the Mississippi and Minnesota river valleys; the stream is deflected upward at two sharp bends in the river valleys where the wind collides with steep 90-m (250–300-ft) valley sideslopes. Paths of severe thunderstorms and tornados coincide to a large degree with these zones of increased precipitation. In Missouri, convective storms that developed in, or passed over, hilly landscapes produced as much as 70% more rainfall than rain cells that were not associated with this type of terrain. Forced uplift and convergence of wind above the hills in response to topography causes intensification of hill-centered storms. In such cases, the resulting rainfall pattern may be more like that occurring over large-scale features, that is, with a leeward maximum.

**Unique physiography.** In areas smaller than 5 km<sup>2</sup> (2 mi<sup>2</sup>) with relief less than 100 m (330 ft) research indicates that rainfall distribution is influenced by unique wind-flow patterns induced by local topographic features. In a level plain surrounded by low hills, rainfall was observed to increase in the direction of airflow along the plain and into the hills. Other researchers have measured greater precipitation in areas subject to concentrated wind flow. In one case, channellike topographic features gathered and conducted airflow toward the higher rainfall locations.

**Windblown raindrops.** For small-scale landforms, those hills and ridges with narrow summits can experience an additional local perturbation in rain distribution. Studies have shown that a consistent pattern of rainfall variability occurs along a path defined by the flow of wind over such ridges or hills. Frictional drag forces of moving air act on raindrops, causing them to drift in the direction of airflow. In the summit region, changes in windspeed and vertical direction alter the inclination angle of falling raindrops. This change in turn modifies amounts of rainfall received at the Earth surface, because rainfall intensity is a function of surface slope and orientation with respect to the direction of falling rain.

At larger landscape scales, rainfall is commonly measured by using a gage with a horizontal opening (meteorological rainfall). When comparing rainfall at small scales it is more appropriate to record the depth of rain actually received on the sloping Earth surface (hydrological rainfall). These measurements more accurately portray subtle rainfall differences that occur when relief varies over short distances. Hydrological rainfall is measured by using a gage with an opening oriented parallel to the Earth surface. For purposes of areal comparisons, hydrological rainfall from a sloping landform facet may be projected onto an equivalent horizon-

tal area (map), and termed the hydrological projected rainfall.

Research has shown that, on a ridge with 40-m (130-ft) relief, hydrological projected rainfall (given as a percentage of the spatial mean) is at a maximum on the windward lower slope and decreases to 100% just leeward of the summit. From that point rainfall continues to decrease, but at a reduced rate, toward the lower leeward slope. Meteorological rainfall behaves in an opposite manner, starting at a minimum and increasing to the leeward.

**Microscale impacts.** Spatial rainfall variation at the microscale is produced by wind-terrain effects on raindrop trajectory. Field studies have shown that the velocity of surface wind flowing across a hill decreases near the windward foot slope, then increases to a maximum near the summit. Wind speed then decreases to a value that may be slightly below incident velocity at the leeward foot slope. The original speed is recovered at a distance of about 1½ hill widths leeward of the summit. A drift effect results when patterned wind flow alters local raindrop incident angles and therefore measured meteorological rainfall and hydrological rainfall intensities.

An instrumented full-scale hill model was recently developed, permitting researchers to conveniently measure microscale wind-terrain impacts. The spatial pattern produced by these interactions varies depending on the overall rainfall intensity, incident wind speed, and hill summit elevation. The locations of maximum and minimum hydrological rainfall across the instrumented hill apparatus can be generalized for cyclonic storms (low-intensity rainfall) and for convective storms (high-intensity rainfall) from data representing several incident wind speeds and summit elevations. On average, locations with maximum hydrological rainfall receive 1½ times more rainfall than locations with minimum rainfall. The magnitude of this variation is significant for hills with such slight relief. These rainfall differences, especially if they occur when crop or soil sensitivity to water inputs is high, can influence spatial patterns of seed germination or seed or fruit development and affect yields; or they can impact on spatial infiltration or soil detachment and transport patterns, and hence on soil erosion.

For rain-fed agricultural lands, it may be economically beneficial to manage soils in high-rainfall areas of the landscape differently from those in low-rainfall areas. Further research defining how topographically induced rainfall patterns influence crop growth and other soil and landscape processes is warranted.

For background information SEE *AIR MASS*; *MOUNTAIN METEOROLOGY*; *PRECIPITATION (METEOROLOGY)*; *RAIN SHADOW*; *WIND* in the McGraw-Hill Encyclopedia of Science & Technology.

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### Prehistoric domestication of animals

The domestication of plants and animals made possible the development of civilizations by permitting human groups to directly control the availability of food resources and to produce food surpluses sufficient to support craft specialists and urban populations not directly engaged in subsistence activities. Archeological research over the past half century has demonstrated that domestication occurred independently several times in different parts of the world, in each case involving locally available plant and animal species. Archeological evidence points to the Near East as the oldest center of domestication, the process beginning there as early as about 10,000 years ago.

**Near Eastern domesticates.** The cultures inhabiting the Near East at the end of the Pleistocene exploited a wide array of wild plant foods, including the seeds of grasses, pulses (legumes), and nuts. They supplemented these plant foods by hunting a variety of game animals. From approximately 10,000 to 8000 years before present (B.P.) several plant and animal species were domesticated in the context of a transition from economic systems based on hunting and gathering to those based on food production. Of those species first domesticated for use as foods, the most important plants were cereal grasses of the genera *Triticum* (wheat) and *Hordeum* (barley), as well as pulses of the genera *Pisum* (field pea) and *Lens* (lentil). The most important of the animal domesticates were sheep (*Ovis*), goats (*Capra*), cattle (*Bos*), and pigs (*Sus*). Not all these species were domesticated concurrently; nor were all first domesticated within the same parts of the Near East. Among the earliest domesticated species were the cereal grasses and the ovicaprids.

The archeological evidence indicates that the cereal grasses were first domesticated approximately 10,000 B.P. by inhabitants of the relatively well-watered eastern Mediterranean seaboard (the Levant). From this core area, domesticated cereals, along with agricultural methods, appear to have rapidly spread to the surrounding highlands of eastern Anatolia, northern Iraq, and western Iran—the Taurus-Zagros arc. The evidence for the domestication of sheep and goats is sketchier, and points to a reverse of this pattern: the domestication of these species seems to have first taken place along the Taurus-Zagros arc, with domesticated ovicaprids subsequently spreading south into the Levant by 8000 B.P. Unfortunately, the relative paucity of excavated sites in the highlands has made it difficult to determine when exactly the domestication of sheep and goats took place. How-

ever, the evidence did suggest that they were the earliest animals domesticated for food in the Near East, with pigs following.

**Sheep and goats.** The greater economic importance of sheep and goats as compared to pigs at later prehistoric and historic sites in the Near East is well documented. It is believed that the preference for herding of sheep and goats over herding of pigs stems primarily from the fact that they can be more easily controlled. Thus, fewer people are needed to herd comparably sized groups of sheep and goats, enabling the maintenance of larger herds. Further, compared to pigs even large herds of sheep and goats can be more easily kept from foraging in stands of wild or cultivated cereals intended for human consumption.

Until recently, the data from the few excavated early sites along the flanks of the Taurus-Zagros arc indicated that, as in the Levant, the preagricultural inhabitants of this area also relied extensively on wild cereals for their subsistence. Thus, the conclusion that sheep and goats were the earliest economically important animal domesticates made theoretical sense and was generally consistent with the available data.

According to that view, along the Taurus-Zagros arc, there was a shift from mobile hunting and gathering to an increasingly settled mode of life, based on either the exploitation of wild cereals (earlier than 10,000 B.P.) or on the introduction of cereal domesticates and agriculture from the Levant (after 10,000 B.P.). Where possible, such increased sedentism resulted in attempts to compensate for local overexploitation of wild animals in the vicinity of now-permanent villages by attempts at animal husbandry. In the Levant, where the most economically important wild animal resource was the gazelle (*Gazella*), animal husbandry may not have been feasible or, if it was, did not lead anywhere. Along the Taurus-Zagros arc (the natural habitat zone for wild sheep and goats) it led to the domestication of these species and the subsequent spread of domesticated sheep and goats south into the Levant.

Controversial evidence from the site of Zawi Chemi in northern Iraq, excavated in the 1950s, was originally interpreted to suggest that the process of ovicaprid domestication was already under way as early as 11,000 B.P. However, subsequent excavations in this region at the sites of Çayönü and Ganj Dareh suggest that the domestication of sheep and goats may not have occurred until after 10,000 B.P. Of equal interest, but until now largely ignored for lack of corroborating evidence from other sites, was the discovery at Çayönü in eastern Anatolia that domesticated pigs were being exploited at least as early as domesticated ovicaprids.

**Pigs.** Recent discoveries at the site of Hallan Çemi in the Taurus foothills of eastern Anatolia now indicate that the domestication of pigs actually preceded that of ovicaprids along the Taurus-Zagros arc. The site of Hallan Çemi is the remains